

**THE IMMATURE STAGES AND BIOLOGY OF THE  
CRANEFLIES *TOXORHINA CALEDONICA* AND  
*ELEPHANTOMYIA GARRIGOUANA* (DIPTERA:  
LIMONIIDAE)**

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*Abstract.*—The larval and pupal stages of the craneflies *Toxorhina* (*Ceratocheilus*) *caledonica* Alexander and *Elephantomyia* (*Elephantomyia*) *garrigouana* Alexander are described. The habitat and certain biological behaviors of *Toxorhina* and *Elephantomyia* are noted. Similarities and differences in structure of the immature stages of the two genera are listed and their importance in the determination of relationships discussed. The characters support a close relationship of the two genera, and confirms the placement of the two genera within the Eriopterini. A possible error in the rearing of one species of *Elephantomyia* from South Africa is also discussed.

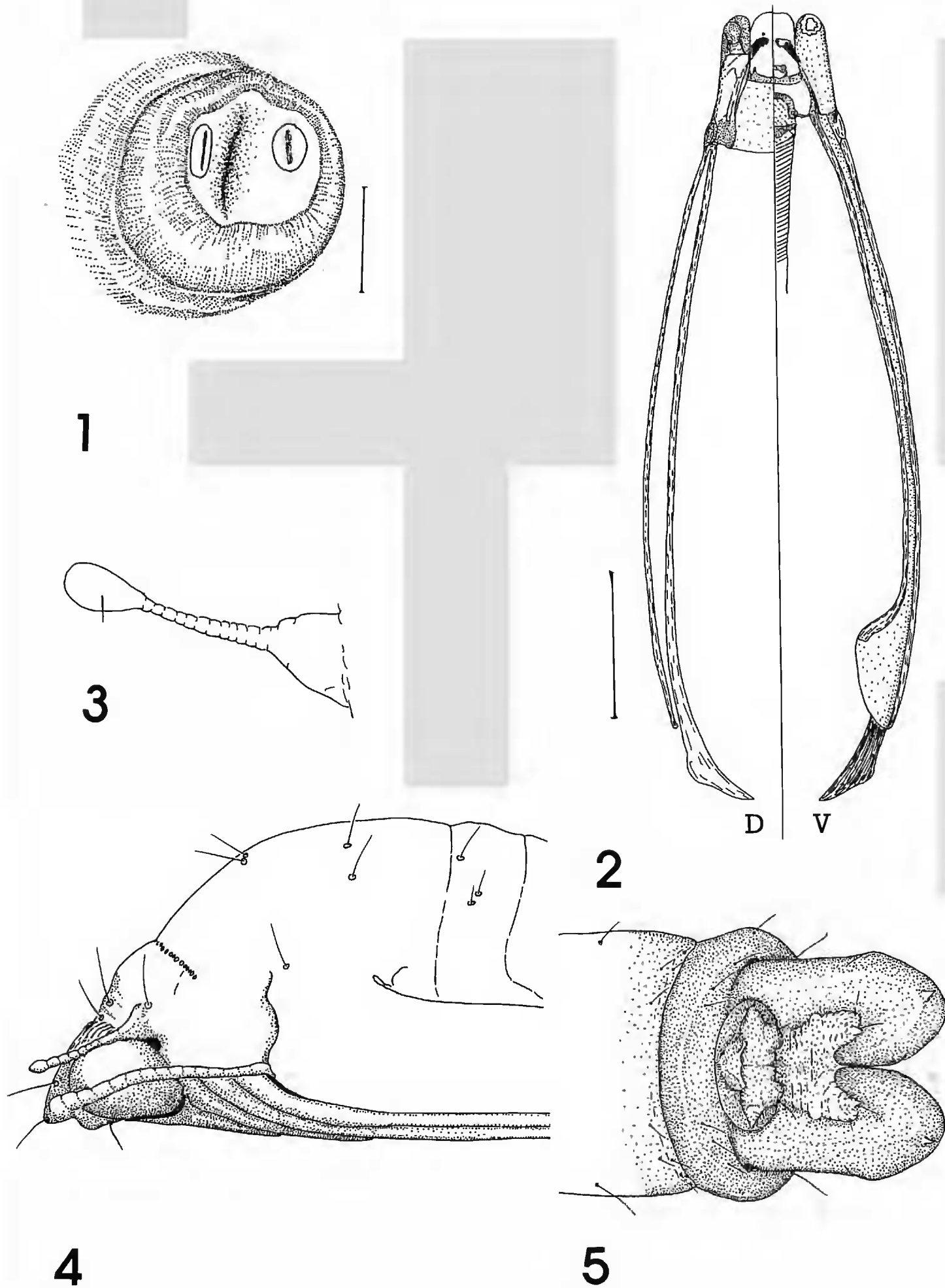
*Key Words.*—Insecta, Diptera, Cranefly, Limoniidae, *Toxorhina*, *Elephantomyia*, larva, pupa, relationship.

The relationship between the genera *Toxorhina* Loew and *Elephantomyia* Osten Sacken and their placement in the present hierarchy of the Limoniidae has been in question for some time. Using adult characters, Alexander (1921a, 1921b) considered these genera to be closely related and, on this supposition, placed both genera in the tribe Eriopterini. Later, Alexander (1923) had transferred the genus *Elephantomyia* to the tribe Hexatomini on the basis of its possession of tibial spurs. *Toxorhina*, without tibial spurs, remained in the Eriopterini. Subsequently, other species of *Elephantomyia* were discovered not having tibial spurs, and the subgenus *Elephantomyodes* (Alexander 1923) was erected to include these species. However, Alexander (1951) described *Elephantomyia* (*Elephantomyia*) *garrigouana* as lacking tibial spurs, yet placed it into the subgenus *Elephantomyia* rather than *Elephantomyodes* on the basis of wing venation. He failed to indicate the exact differences in wing venation that led him to this conclusion. This further confused relationships within *Elephantomyia* and also between *Elephantomyia* and *Toxorhina*. The confusion was compounded by a probable error by Wood's (1952) rearing of a South African species of *Elephantomyia*. Since the immature stages of *E.* (*Elephantomyia*) *westwoodi* O. S. had been described earlier (Alexander 1921a) and other species later (Bangerter 1934, Savchenko 1986, Wood 1952) it was hoped that discovery of the immature stages of the genus *Toxorhina* would supply information to clear up the matter.

In New Caledonia I found and reared the immature stages of *Toxorhina* (*Ceratocheilus*) *caledonica* Alexander. For comparison I include a description of the immature stages of *Elephantomyia* (*Elephantomyia*) *garrigouana* Alexander.

*Toxorhina* (*Ceratocheilus*) *caledonica* Alexander  
(Figs. 1-5)

*Larva.*—Body cylindrical, cigar shaped posteriorly, tapering anteriorly, covered with dark setae giving body a gray velvet sheen. Spiracular disk (Fig. 1) without lobes, outer border a rounded collar, dorsomedial area slightly indented; face of disk and spiracles white. Spinous ventral creeping welts



Figures 1-5. *Toxorhina (Ceratocheilus) caledonica* Alexander; scale indicators (when present) are 0.1 mm. Figure 1. Spiracular disk, posterolateral view. Figure 2. Larval head capsule (d-dorsal, v-ventral). Figure 3. Mesothoracic breathing horn. Figure 4. Male pupa, anterior end, lateral view. Figure 5. Male pupa, posterior end, dorsal view.

on abdominal segments 6 and 7. Anal gills or lobes absent. Abdominal segment 10 a white mound with the anus at its anterior border. Both anus and mound (mound similarly shaped to, but definitely not a creeping welt and not spinous) covered by anterior flap of elongate, dark gray setae. Head capsule (Fig. 2): length from anterior tip of labrum to posterior margin of dorsal plate 0.51 mm; width at mandibular articulation 0.08 mm. Head very elongate, length/width ratio 6.4; dorsal and dorsolateral bar-like phragmata approximately same width, ventral bars slightly wider apically. Mandible slightly slanted or rotated from vertical plane, recurved distally, ending in small teeth. Area behind clypeus entirely membranous. Anterior portion of esophagus sclerotized, with riblike structures for a short distance posteriorly. Maxillae blunt; antennae short, terminal papilla same size as sclerotized basal segment. Length 9.3 mm; width at fourth abdominal segment 0.95 mm.

*Pupa*.—Body light brown, long, narrow. Antennal sheath lying directly across eye (Fig. 4). Small crest or row of folds between bases of antennae, another row at posterodorsal margin of eye; a large tubercle directed forward, ending in an elongate seta between antennal bases. Mesothoracic breathing horns (0.8–1.1 mm) extending laterally, slightly widened at base becoming narrower then again widening just before tip, constrictions along shaft, tip slightly enlarged, oval, flattened dorsoventrally (Fig. 3). Wing pads nearly black in more mature specimens. Mesothoracic leg sheaths slightly wider than others, ending just before posterior edge of abdominal segment 6, mesothoracic leg sheaths only slightly shorter; metathoracic sheaths much shorter, ending at no more than midlength of abdominal segment 6. Abdominal segments punctulate. Segments 2–7 with three rings, two narrow basal rings and one broad distal ring. Male cauda (Fig. 5) with segment 8 forming collar, folded over anterior edge of segment 9. Sternite 9 bulbous, smooth; tergite 9 with anterior oval area with two strong, rounded tubercles and two teeth, one extending laterad on each side. Sheaths of dististyles strongly recurved; a sharp tooth in angle of curvature bearing a strong seta, another short tooth on caudal edge. Length 6.9–7.0 mm; dextrosinistral and dorsoventral width at wing base 0.9–1.1 mm.

The description of *Toxorhina caledonica* is based on four larvae and three pupae, deposited in my collection.

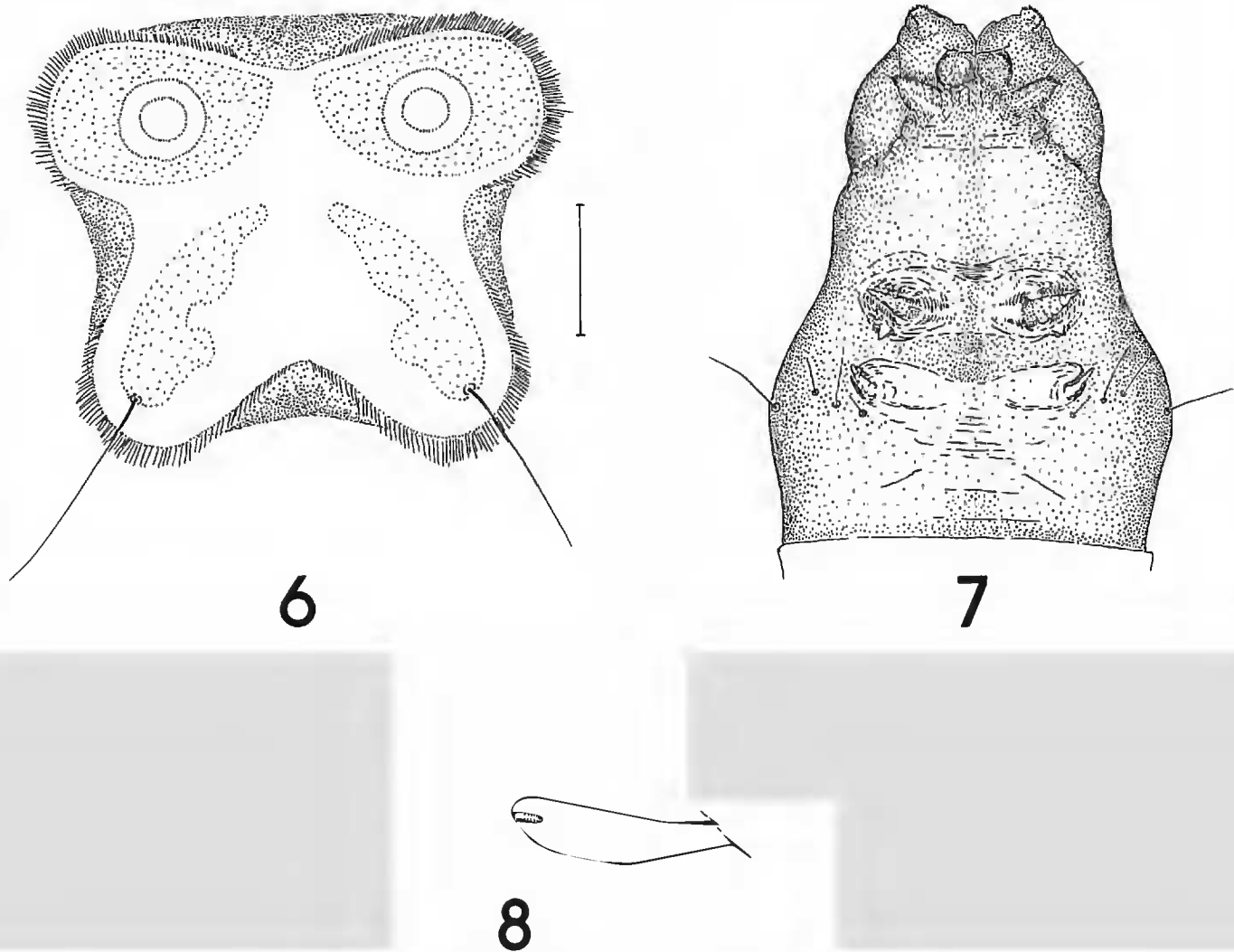
*Specimens Examined*.—NEW CALEDONIA: Riviere Bleue; 10-1788-1.1, 10-1788-1.2. To avoid confusion, these numbers represent my catalog number as well as the rearing cage number. This number also indicates the vial in which the reared specimens are found (month 10-day 17 of year 1988-microhabitat 1 and specimen or specimens reared .2) This format is followed throughout this paper.

*Elephantomyia (Elephantomyia) Garrigouana* Alexander  
(Figs. 6–8)

*Larva*.—Body cylindrical, covered with closely appressed golden setae. Spinous ventral creeping welts present on abdominal segments 5, 6, and 7. Spiracular disk (Fig. 6) with 4 lobes, ventral ones slightly longer, each with an elongate, stout seta extending caudad; outer edge of all lobes with fringe of setae; face with light brown markings, spiracles gold. Anal gills or lobes absent. Abdominal segment 10 with anus at anterior border of small, white mound, both covered with a row of dense elongate setae originating along anterior edge of anus. Head capsule very slender, elongate, length 0.33–0.41 mm; width at mandibular articulation 0.05–0.06 mm; L/W ratio 6.3 to 6.5. Six “bars” or “rods” with membranes forming 3 plates; dorsal and ventral bars approximately same size, the dorsolateral ones more slender, becoming extremely thin at posterior end. Mandible slightly slanted or rotated from vertical axis, not recurved distally, ending in rounded teeth. Postclypeal area entirely membranous. Anterior portion of esophagus with sclerotized, riblike structures. Maxillae blunt; antennae short, terminal papilla larger than basal segment. Length 7.7–9.1 mm; width at fourth abdominal segment 0.7–0.79 mm.

*Pupa*.—Antennal sheaths lying across eyes. Mesothoracic breathing horn (0.30–0.37 mm) elongate, clavate, flattened laterally, extending cephalad (Fig. 8). Wing pads end at posterior edge of abdominal segment 2. Mesothoracic leg sheaths slightly enlarged at base, ending at three-quarters length of abdominal segment 5, mesothoracic sheaths slightly shorter, metathoracic sheaths still shorter. Dorsally, abdominal segment 9 bearing 4 sharply pointed lobes, anterior pair thinner than posterior pair. On caudal edge of each dististyle sheath a short, curved row of spines. Four lobes anterior to dististyle sheaths posterior pair spherical, anterior pair pointed, tips with several spinules and 2 seta directed laterad (Fig. 7). Length 5.1–5.4 mm; dextro-sinistral and dorso-ventral width at wing base 0.7–0.8 mm.

The description of *E. garrigouana* is based on twelve larvae and three pupae and are deposited in my collection.



Figures 6-8. *Elephantomyia (Elephantomyia) garrigouana* Alexander; scale indicator (when present) 0.1 mm. Figure 6. Spiracular disk. Figure 7. Male pupa, posterior end, dorsal view. Figure 8. Mesothoracic breathing horn.

*Specimens Examined.*—NEW CALEDONIA: Mont Mou; 10-1888-1.2, 11-1588-1.1. Riviere Blanc; 11-888-1.2. Riviere Bleue; 10-2788-1.5a, 11-1788-1.2 (See above for explanation of numbers).

#### BIOLOGY

*Habitat.*—The larvae of both *Toxorhina (Ceratocheilus) caledonica* and *Elephantomyia (Elephantomyia) garrigouana* were found in two general habitats. The first is rotting branches of trees (Myrsinaceae, probably *Rapanea*) beneath accumulations of twigs and leaves. Those of *T. caledonica* were taken from rotted wood that was slimy, not punky, indicating a much more advanced stage of decay than that in which the larvae of *E. garrigouana* were found.

The second habitat was rotting palm fronds. Larvae were located in a brown, syrupy liquid between the fibers of the petiole. The larvae of *T. caledonica* were found in the wet proximal areas of the petiole; those of *E. garrigouana* were found in drier, more distal areas of the petiole. The pupae of both species were found in dryer areas of both habitats.

*Elephantomyia garrigouana* was also found in punky wood Araiaceae (either *Myodocarpus*, or more probably *Schefflera*). The immature stages of *T. caledonica* were not found in this habitat.

*Emergence.*—The pupal period of both species was approximately seven days in ambient temperatures (range: 22–25° C). At emergence, the teneral adult of *T. caledonica*, is engorged with water and air and the abdomen is very elongated. The rostrum of the head at eclosion is short, and barely reaches back to the base

of the wing. In five to ten minutes after complete emergence from the pupal case, the rostrum starts to elongate, becoming longer than the entire body. This is accomplished by hydrostatic pressure within the body before hardening of the exoskeleton.

#### DISCUSSION

There are no differences between the larvae or pupae of *E. garrigouana* and *E. westwoodi* that would indicate that the presence or absence of the tibial spur (absent in the adult of the former) should lead to the erection of a new subgenus. In fact, the differences are so slight as to lead one to disregard the subgenus *Elephantomyodes* altogether, placing species with or without tibial spurs in the subgenus *Elephantomyia*.

The most obvious difference between the larvae of *Elephantomyia* and *Toxorhina* is found in the structure of the outer edge of the spiracular disk, i.e., the lack of discal lobes in *Toxorhina* and their presence in *Elephantomyia*. Both genera have an anal mound directly posterior to the anus and a transverse and heavy row of elongate setae forming a "flap" over the anus and the anal mound. Although similar in shape, the mound is definitely not a creeping welt and must serve the same purpose as the anal gills. Dissection reveals that gills are not retracted or present within the anal area of either genus. Also notable is the presence of ventral creeping welts on abdominal segments 5, 6 and 7 in *Elephantomyia*, but on only 6 and 7 in *Toxorhina*. Similarities indicating the close relationship of the two genera are numerous.

The head capsules are very similar in their structural features. All specimens of *E. garrigouana* and *T. caledonica*, as well as *E. westwoodi*, have head length/width ratios of well over 5.0. This ratio is taken as the length of the head from the anterior edge of the labrum to the posterior edge of the dorsal plate, divided by the width of the head capsule at the posterior or outer articulation of the mandibles. The measurement indicates the very slender appearance of the head capsule when compared to those of all other larvae of the Tipulomorpha, which have length/width ratios (from this measurement) under 4.0.

The antennal buttress in *Elephantomyia* and *Toxorhina* is elongate compared to that of other genera. The shape and relative size of the papilla to the basal segment of the antennae are nearly the same in both genera. The dorsolateral bar or rod-like phragmata is much thinner in *Elephantomyia*.

The mandibles are very small (about 0.02 mm long in *E. garrigouana*; 0.04 mm in *T. caledonica*) and slightly turned downward allowing for a scraping movement. Alexander (1921a) described the mandibles of *E. westwoodi* as pointed with the inner surface toothed. Specimens that I dissected have a rounded tip with additional teeth on the inner edge. The mandibular structure of *Toxorhina* is slightly more complex than that of *Elephantomyia*, but in both cases it indicates a scraping action in the procurement of food. The slight tilt to the mandibles perhaps explains their unusual position in Alexander's drawing (Alexander 1921a).

A striking resemblance between the two genera is the presence of the ribbed anterior portion of the esophagus. No other known genera within the Tipulomorpha have such ribbing. The closest approximation would be the spines in similar locations in some hexatomine groups. The purpose of this structure is unknown, but it may protect the forward portion of the esophagus from sharp edges found in the food ingested.

The structural similarities between the larval, pupal and adult forms of the two genera are summarized as follows. From the larvae: (1) the length/width ratio and shape of the head capsule; (2) the size and shape of the antennae; (3) the size and shape of the mandibles; (4) the tilt or slant of the mandibles; (5) the presence of ribbing in the forward part of esophagus; and (6) the structure of the anus, anal mound and covering setal "flap".

From the pupae: (1) the antennal sheath lying across the eye dividing the eye sheath into two parts, not across the dorsal border of the eye sheath as in most other tipulids; and (2) the similar ecological habitat.

The similarities of the immatures suggest that the two genera are closely related and should be placed in the same grouping of the hierarchy. I have already indicated in an earlier paper (Hynes 1993) that both should be placed in the Eriopterini. This suggestion ignores the presence or absence of tibial spurs. Without getting into a discussion of the differences between "key," "evolutionary," and "cladistic" characters, I feel that the character "tibial spur" as currently used is best removed from discussions of relationship.

Oosterbroek and Theowald (1991) infer that the genus *Elephantomyia* might be placed in limoniine groups. This is based on the immatures of one species, *E. aurantica*, supposedly reared by Wood (1952). Wood indicated that this species has a larva apparently limoniine in form, not eriopterine as in the other species he reared. Several aspects of this conclusion are disturbing. Such discussions are often accepted to a degree that details tend to take on the aura of undisputed data, and such must be avoided in this case. The primary reason is the reported condition of rearing the species. If one reads the account by Wood, the conclusion must be reached that other individuals did the rearing. Only one larva was reared to the pupal stage, and there is no mention as to whether this pupa was reared to adult. Also one must conclude that there was no attempt to control the medium in which the rearing was accomplished. When collecting, one finds other larvae, particularly the genus *Limonia*, in the same habitat as *Elephantomyia* and *Toxorhina*. Moreover, a given species is not necessarily found in only one habitat (see above). Care must be taken that the larva one wishes to rear is the only type of larva present. Failure to observe these cautions allows a large probability of error. But further than that, to allow that a gene complement could change so drastically (as in Wood's *Elephantomyia* larva), yet have no real effect on differentiation in later development (pupa and adult) is very improbable. Convergent evolution is an extremely rare event and in no case so perfectly matched in two of the three developmental stages. That someone made mistakes in rearing technique has a much greater probability and is far more believable. The rearing must be repeated, and in such a manner that there can be no doubt as its validity, i.e., a definite association of one larva to its pupa and subsequently to its adult. Until this is accomplished, suppositions on monophyly or polyphyly based on Wood's data on *E. aurantiaca* should not be made.

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